

## Correspondences

## Male chimpanzees exchange political support for mating opportunities

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Male chimpanzees, *Pan troglodytes*, differ from males in most other mammalian taxa because they remain in their natal communities throughout their lives, form close bonds with one another, and cooperate in a range of activities [1]. However, males also compete fiercely for status within their groups [2,3], and high rank enhances male reproductive success [4,5]. Males rely partly on coalitions to achieve and maintain status [2,3,6–9], and shifts in male alliances can have dramatic political effects [2,3,6]. It is not known what benefits are obtained by low-ranking coalition partners. Here we report that the highest-ranking (alpha) male in one well-studied community of chimpanzees rewarded his allies by allowing them preferential access to mates.

During the 22-month study period, the Kanyawara community of chimpanzees contained ten mature males. The males were ranked in a linear dominance hierarchy that remained stable during the study period. The highest-ranking male, MS, had held the alpha position for four years when the present study began in 2001 and retained this position throughout the study.

Six parous females became sexually receptive and began to cycle regularly during the study period. Parous females are more attractive than nulliparous females as mating partners [10]. Females are most likely to conceive when their sex skins are fully swollen, and male mating activity is highest during this period [10]. Thus, we considered females to be sexually 'attractive' on a given day if they were parous, their sex skins were

maximally swollen, and they were the objects of male–male mating competition on that day. Only matings and interferences in copulations with attractive females are considered below. (For additional information see the Supplemental data available on-line with this issue).

The alpha male, MS, monopolized access to attractive females. MS was responsible for twice as many copulations as any other male (32%,  $N = 234$  copulations by all males), and he was also responsible for the majority of interferences when other males tried to mate (52%,  $N = 109$  interferences by all males). Overall, males interfered in 34% of the 323 mating attempts observed, and interference usually prevented copulations from being completed ( $89/109 = 82\%$ ).

The mating success of lower-ranking males was strongly affected by their support of the alpha male. MS received 58 acts of support from other males, and all but one of the mature males supported MS at least once (range: 0–19 supports). MS was most tolerant of the mating attempts of males that supported him most frequently in conflicts ( $r_s = 0.800$ ,  $n = 9$ ,  $p = 0.010$ ), and the males that most often supported MS also copulated more often than other males ( $r_s = 0.812$ ,  $n = 9$ ,  $p = 0.008$ ).

These results might be an artifact of male dominance rank because MS was most often supported by high-ranking males who also have high mating success (support  $\times$  rank:  $r_s = -0.800$ ,  $n = 9$ ,  $p = 0.010$ ; mating success  $\times$  rank: all males:  $r_s = -0.802$ ,  $n = 10$ ,  $p = 0.005$ ;

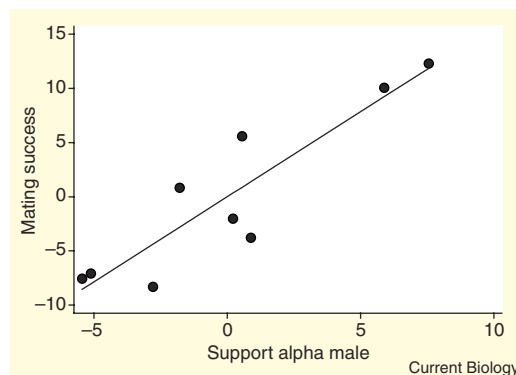
excluding MS:  $r_s = -0.686$ ,  $n = 9$ ,  $p = 0.041$ ). The sample of mature males is too small to conduct multivariate analyses, but we can assess the relative importance of dominance rank and support of MS on male mating success by examining the partial regression plots. Figure 1 shows that support of MS is strongly linked to male mating success, when the effects of male rank on mating success are controlled statistically. At the same time, male dominance rank has relatively little impact on male mating success when support for MS is controlled statistically (Figure 2).

These results show that the alpha male in the Kanyawara community selectively tolerated mating by his allies and exchanged mating tolerance for support in conflicts. The alpha male in this community was a singularly important trading partner because of the disproportionately high value of his mating tolerance.

In chimpanzee communities, alpha males rely on support from subordinates to maintain their status [3,6–8]. The most valuable currency controlled by the alpha male is access to mates. By selectively rewarding his allies with tolerance of their mating efforts, the alpha male may discourage potential rivals from mounting challenges against him: rivals will not only have to defeat the alpha male and his allies, they will also forfeit future mating opportunities if their challenges are unsuccessful. The ability to form these kinds of strategic coalitions may allow some male chimpanzees to maintain alpha status for relatively long periods of time.

Figure 1. Effect of agonistic support given to alpha male on mating success when dominance rank is controlled statistically.

Mating success was measured as the number of copulations with attractive females. Values of mating success are based on residual values derived from the regression model.



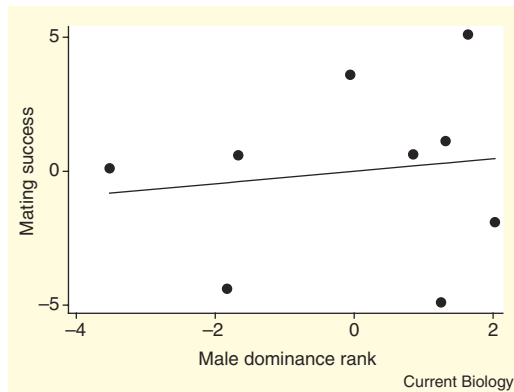


Figure 2. Effect of male dominance rank on mating success when support for alpha male is controlled statistically. Mating success was measured as the number of copulations with attractive females.

Values of mating success are based on residual values derived from the regression model.

These data suggest that cooperative tactics among male chimpanzees are as important as rank competition in determining male mating success. The alpha male at Kanyawara had much higher mating success than other males, but still allowed his allies preferential access to mates. This strategy probably extended his tenure by retaining allies who consistently supported him. For the alpha male, these lost mating opportunities may be the price of power. For his allies, the benefits derived from supporting the alpha male may be more important than achieving high status.

#### Supplemental data

Supplemental data including experimental procedures are available at <http://www.current-biology.com/cgi/content/full/17/15/R586/DC1>

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## Modulation by dopamine of human basal ganglia involvement in feedback control of movement

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We learn new motor tasks by trial and error, repeating what works best and avoiding past mistakes. To repeat what works best we must register a satisfactory outcome, and in a study [1] we showed the existence of an evoked activity in the basal ganglia that correlates with accuracy of task performance and is associated with reiteration of successful motor parameters in subsequent movements. Here we report evidence that the signaling of positive trial outcome relies on dopaminergic input to the basal ganglia, by recording from the subthalamic nucleus (STN) in patients with nigrostriatal denervation due to Parkinson's Disease (PD) who have undergone functional neurosurgery. Correlations between subthalamic evoked activities and trial accuracy were weak and behavioral performance remained poor while patients were untreated; however, both improved after the dopamine prodrug levodopa was re-introduced. The results suggest that the midbrain dopaminergic system may be important, not only in signaling explicit positive outcomes or rewards in tasks requiring choices between options [2,3], but also in trial-to-trial learning and in reinforcing the selection of optimal parameters in more automatic motor control.

We studied seven patients with PD in whom the STN was